A BIOSYSTEMATIC STUDY OF *SILPHIUM INTEGRIFOLIUM* MICHAUX (COMPOSITAE)[1, 2]

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ABSTRACT

Cytological and chromatographic data indicate that *Silphium integrifolium* Michx. is a rather homogeneous group of plants. Cytological study shows good pairing during meiosis in interspecific and intraspecific hybrids. Two-dimensional paper chromatography indicates that the varieties of *S. integrifolium* are more similar to each other than they are to two related species, *S. asperrimum* and *S. speciosum*. The varieties of *S. integrifolium* are chromatographically homogeneous.

INTRODUCTION

For several years the genus *Silphium* has been studied by the junior author, and several of his students have investigated some of the species. Anderson (1968) worked on *S. laciniatum* L. and *S. albiflorum* Gray; Cruden (1962) studied *S. perfoliatum* L.; Lengel (1963) investigated *S. integrifolium* Michx., *S. speciosum* Nutt., and *S. asperrimum* Hook.; Sweeney (1970) studied *S. compositum* Michx.; and Weber worked on *S. asteriscus* L.

The results reported in this paper represent a part of a study of *Silphium intergrifolium* Michx. *Silphium integrifolium* and *S. speciosum* are sympatric in the Oklahoma-Texas-Arkansas area. Naturally occurring putative hybrids between *S. integrifolium* and *S. speciosum* and between *S. integrifolium* and *S. asperrimum* have been found, all of which are morphologically similar. This study focuses upon the relationship between these three species.

Silphium integrifolium is a morphologically homogeneous group of plants and has been separated into varieties on the basis of the kind and extent of vesture on the phyllaries and on the lower surface of the leaves (Settle and Fisher, 1970).

CYTOLOGICAL ANALYSIS

Cytological observations were made of microsporocytes undergoing meiosis in the stamens of the tubular flowers in order to study chromosome pairing and to detect any meiotic abnormalities. The flower buds used were collected from plants growing in the research garden of The Ohio State University, where the *Silphium* research was initiated. These plants were collected and transplanted there, or started there from seed, by the junior author.

The flower buds were fixed in a solution of 100% ethanol: glacial acetic acid (3:1) for 24 hours, and were stored in 70% ethanol under refrigeration (3° C) until used. At that time, the anthers were removed from the disk flowers and squashed in iron aceto-carmine. Permanent slides were made by freezing them on dry ice and removing the cover slip with a razor blade, following the method of Conger and Fairchild (1935). The slides were dipped into a solution of 95% ethanol and then into 100% ethanol for a few seconds and remounted on a clean slide with euparal. Photographs were made from these permanent slides. Vouchers of this material are deposited at the State University of New York, College at Oneonta. Voucher specimens of the plants are deposited in the herbarium of

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Bowling Green State University; the collection numbers cited in this paper are those of the junior author.

All species of *Silphium* which have been studied have a chromosome number of n = 7 (Fisher and Cruden, 1962; Settle, 1967). Although the chromosome number is constant, karyotypes vary from species to species (Settle, 1967). Further, Anderson (1968) has demonstrated that three groups of species can be distinguished on the basis of reciprocal translocations between the longest and shortest chromosomes.

When the hybridization program was begun, certain plants were chosen as typical representatives of each taxon in the genus and designated as standards.

TABLE 1

Collection data for representatives of Silphium integrifolium

Collection Number	Variety	Locality
63	*integrifolium*	Coles County, Illinois
73	*neglectum*	White County, Indiana
147	*integrifolium*	Coles County, Illinois
148	*integrifolium*	Coles County, Illinois
158	*integrifolium*	Coles County, Illinois
160	*integrifolium*	Coles County, Illinois
162	*neglectum*	Iroquois County, Illinois
218	*integrifolium*	Hardin County, Tennessee
219	*deamii*	Shelby County, Tennessee
276	*deamii*	White County, Arkansas
284	*integrifolium*	Phelps County, Missouri
1104	*deamii*	Union County, Illinois
2084	*integrifolium*	Lawrence County, Illinois
2169	*deamii*	White County, Arkansas
2187	*deamii*	Garland County, Arkansas
2189	*deamii*	Saline County, Arkansas
2237	*deamii*	Perry County, Illinois

Silphium reverchonii (90), *S. asteriscus* spp. *trifoliatum* (105), and *S. laciniatum* (200) were chosen arbitrarily as representatives of Groups A, B, and C, respectively. All of the plants in a given group have the same chromosome end-arrangements. When a plant of a given group is crossed with another plant in the same group, the F_1 hybrid has seven bivalents during meiosis. However, if a member of one group is crossed with a member of another group, the F_1 hybrid will have a ring or chain of four chromosomes. Because no hybrids have been found in which the multivalent is composed of more than four chromosomes, it is assumed that the translocations involve different arms of the same chromosome. Because the authors have not determined any evolutionary relationships involving chromosome end-arrangement, it cannot be inferred that one end arrangement is more primitive than another.

The end arrangement characteristic of each of the different species has been inferred from the study of plants resulting from triangulated crosses made by Fisher and several of his students. Crosses involving *Silphium integrifolium* are shown in Figure 1. All but one representative of *S. integrifolium* are in Group B; plant #218 is in Group A. The 17 representatives of *S. integrifolium* used in this study, along with collection data, are given in Table 1. Pairing of the homologous chromosomes seen during diakinesis and metaphase I of the intraspecific and interspecific hybrids was normal (fig. 7).

Although some bridges and fragments were found in the different hybrids, their occurrence was rare. They were found in approximately one percent or less of the microsporocytes examined. In the hybrid between plants #73 (*S. integrifolium*) and #2071 (*S. perfoliatum* var. *connatum*), bridges and fragments did occur in approximately 50 per cent of the microsporocytes (fig. 2). Bridges were found

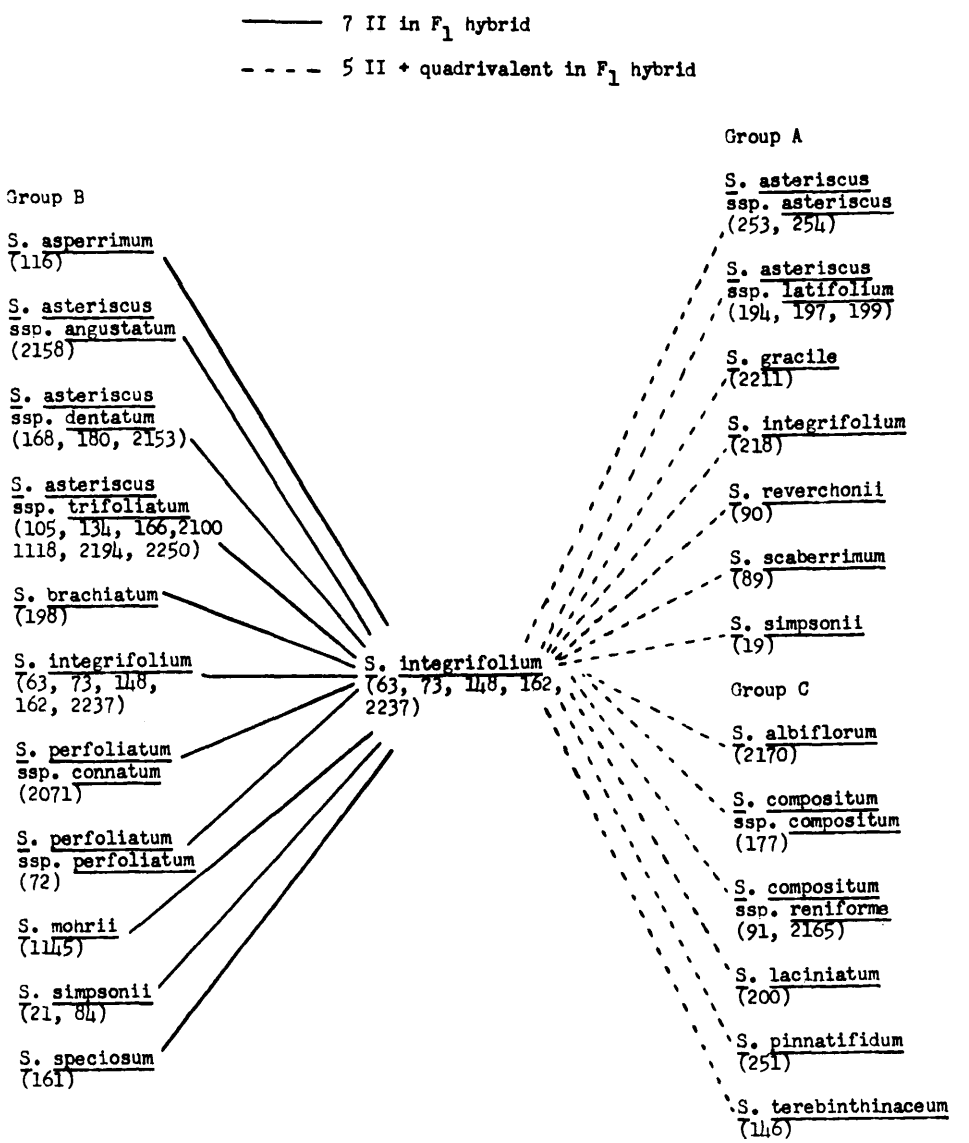
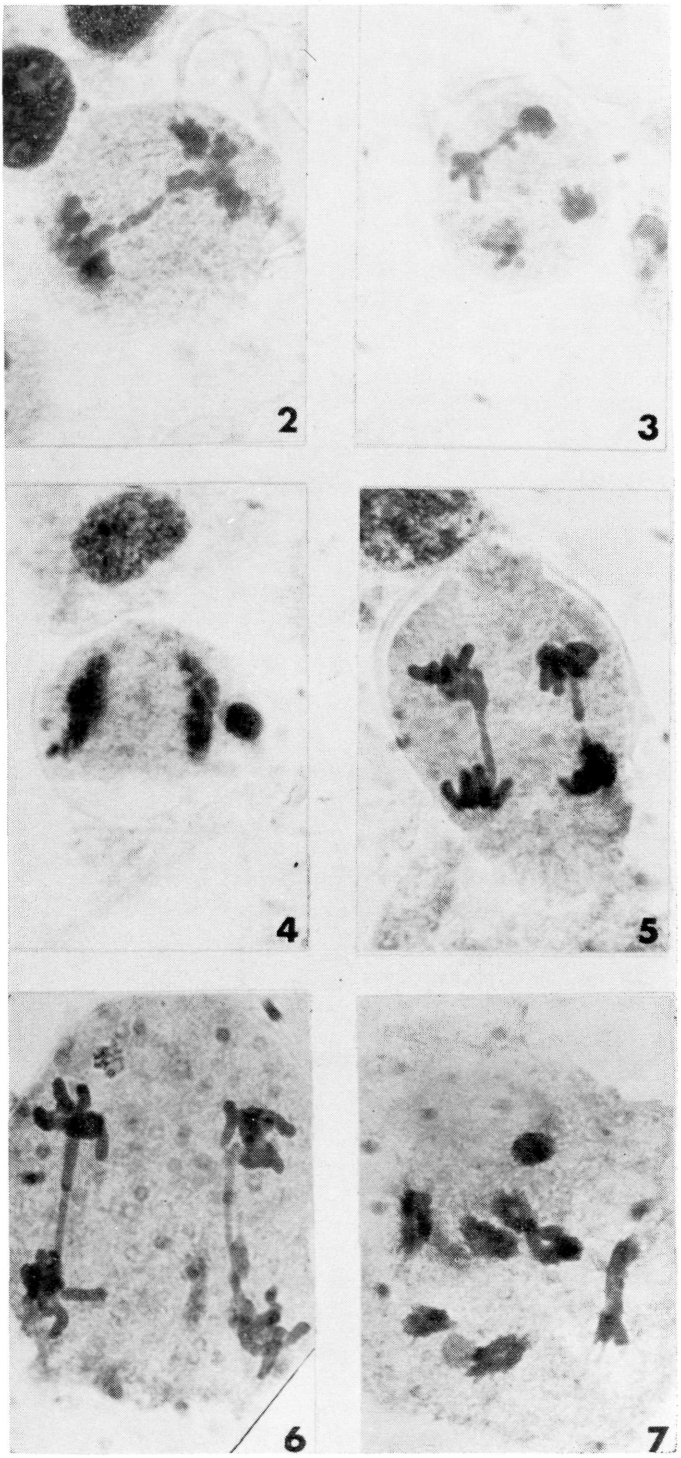


FIGURE 1. Inter- and intraspecific crosses of *Silphium integrifolium* (numbers represent population samples).

EXPLANATION OF FIGURE

FIGURES 2–7. Meiotic cells of *Silphium integrifolium* and hybrids involving *S. integrifolium* (×1125). FIGURE 2. Bridge and fragment, *S. integrifolium* (73)×*S. perfoliatum* var. *connatum* (2071). FIGURE 3. Bridge persisting to Anaphase II, *S. integrifolium* (73)×*S. perfoliatum* var. *connatum* (2071). FIGURE 4. Micronucleus, *S. integrifolium* (73)×*S. perfoliatum* var. *connatum* (2071). FIGURE 5. Bridges without fragments, [*S. integrifolium* (148)×*S. scaberrimum* (89)] ×self. FIGURE 6. Bridges without fragments, [*S. integrifolium* (148)×*S. simpsonii* var. *wrightii* (84)]×*S. simpsonii* var. *wrightii* (84). FIGURE 7. Synapsis, *S. integrifolium* (2169)×*S. integrifolium* (2084).



FIGURES 2–7

persisting to anaphase II in this same hybrid (fig. 3), but micronuclei, which often result from acentric fragments, were observed in some plants containing bridges and fragments (fig. 4). Configurations which appear to be bridges without fragments were found in a few microsporocytes of most plants examined cytologically (figs. 5, 6). It is a ssumed that most of these are tardily separating chromosomes; these "sticky chromosome bridges" do not appear to cause any deleterious effects to the plants, because the homologs separate and meiosis continues in the usual fashion.

Supernumerary chromosomes have been observed in some *Silphium* plants (Weber, 1968; Anderson, 1968). However, no supernumerary chromsomes were found in *S. integrifolium* or in any of the hybrids involving the species studied in this project.

CHROMATOGRAPHIC ANALYSIS

Four to six healthy, mature leaves of each representative of *Silphium integrifolium* were collected from The Ohio State University research graden in June, 1966, and in June, 1968. Similar collections of the two representatives of *S. asperrimum* and *S. speciosum* were made from the research garden in June, 1966. The leaves were dried in paper bags in a room with sufficient air circulation to allow rapid drying. Although there was no control of the temperature in the room, it never rose about 35°C. After approximately a week of drying, the leaves were transferred to 5″ x 7″ manila envelopes, where they were stored until used. At that time, the midrib of each leaf was removed, and the remaining portion of the leaf was ground to a fine powder by use of a large mortar and pestle.

Approximately 0.5 gram of pulverized leaf material was placed in the bottom of a 2¼-in screw-cap vial. To this powder was added 5 ml of 1% HCl in methanol, after which the vial was left in the dark at room temperature for 24 hours for extraction. After extraction, the dark-green solution was decanted and stored in a refrigerator at 3°C for no longer than 3 to 4 days.

Whatman no. 3 MM chromatography paper cut in squares of 15 in x 15 in was used for the paper chromatograms. There was no pre-treating or pre-washing of the paper. An area approximately 1 cm in diameter was spotted with 100 microliters of the extract by use of a 5-microliter capillary pipette.

Large glass jars were used for ascending paper chromatography. The solvent for the first direction was butanol: 27% glacial acetic acid (1:1), and the solvent for the second direction was ethyl acetate: butanone-formis acid-water (5:3:1:1). The total developing distance was 12″ in both directions, and, after drying in a hood for at least one hour, at least three chromatograms of each representative were analyzed.

Each chromatogram was read and marked under the following conditions and in the following order: 1) no reagent, in visible and ultra-violet light; 2) NH_4OH sprayed from aerosal can, in visible and ultra-violet light; and 3) 2% phosphomolybdic acid in 50% acetone, sprayed from aerosol can (Sweeney, 1966) and NH_4OH sprayed from aerosol can, in visible and ultra-violet light. After all of the spots on the chromatograms had been marked and recorded, each spot was characterized by its location and color.

A composite two-dimensional chromatograph showing all of the spots and their relative location is shown in Figure 8. The color reactions of these spots are listed in Table 7. Tables 8 and 9 show in which plants the spots occur.

Chromatographic profiles were constructed for each plant based on three chromatograms of each representative of *Silphium integrifolium*, *S. asperrimum*, and *S. speciosum*, and compared by use of the paired-affinity index (Ellison, Turner, and Alston, 1962). This test compares each chromatographic profile with every other profile, resulting in a series of paired affinity-values ranging from 0 to 100. If two chromatographic profiles do not have any spots in common, their paired

affinity-value is 0, whereas, if the profiles are identical, the paired-affinity value is 100. The paired affinity-values for the varieties of *Silphium integrifolium* are listed in Table 2. Paired affinity-values comparing each representative of *S. integrifolium* with the representatives of *S. asperrimum* and *S. speciosum* are shown in Table 3.

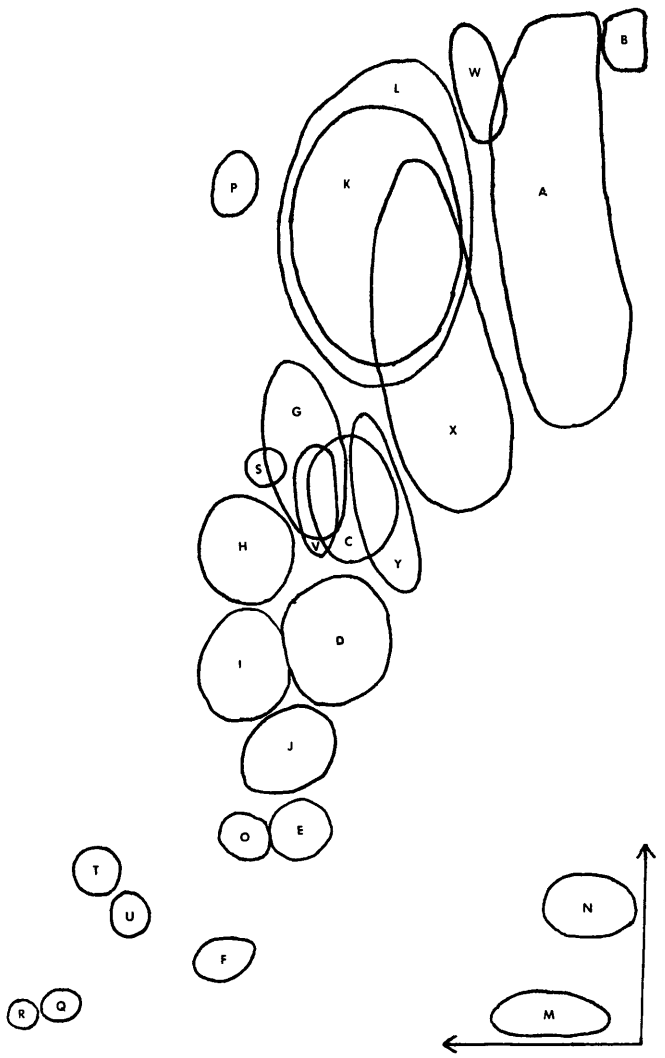


FIGURE 8. Composite two-dimensional chromatograph showing all spots and their relative location.

Three kinds of paired affinity-values were computed in this study: intravarietal, intervarietal, and interspecific. 1) Intravarietal comparisons are those paired affinity-values which were obtained by comparing two chromatographic profiles of the same variety. 2) Intervarietal comparisons are those paired affinity-values obtained by comparing two chromatographic profiles of different varieties. 3) Interspecific comparisons are those paired affinity-values which were obtained by comparing two chromatographic profiles of different species.

TABLE 2

Paired affinity-values between varieties of Silphium integrifolium

	integrifolium								*neglectum*			*deamii*				
	147	148	148–2	158	160	218	284	2084	73	162	219	276	1104	2169	2187	2189	2237
63	77	75	75	62	67	71	64	67	67	71	47	64	64	71	50	77	75
147		82	67	67	60	64	69	73	73	64	50	69	69	69	53	83	82
148			64	64	57	62	67	70	70	62	46	67	67	75	50	82	100
148–2				80	57	75	67	70	89	75	58	67	67	62	62	67	64
158					69	75	92	70	89	75	73	82	82	75	75	82	64
160						67	85	62	62	79	64	85	85	79	67	72	57
218							77	54	67	85	69	77	77	85	72	77	62
284								73	73	92	75	100	100	92	77	83	67
2084									78	66	50	73	73	67	54	73	70
73										67	70	73	73	67	67	73	70
162											69	92	92	85	72	77	62
219												75	75	69	69	62	46
276													100	92	77	83	66
1104														92	77	83	66
2169															72	92	75
2187																64	50
2189																	82

TABLE 3

Paired affinity-values between varieties of Silphium integrifolium (*left column*) *and collections of* S. asperrimum *and* S. speciosum

	S. asperrimum		*S. speciosum*	
	1133	1166	203	161
63	50	40	29	47
147	53	33	24	40
148	50	38	27	36
148–2	62	38	36	58
158	75	38	27	46
160	56	38	21	35
218	60	40	29	47
284	64	43	24	40
2084	54	31	20	38
73	67	31	29	50
162	60	50	29	47
219	57	36	25	43
276	64	43	24	40
1104	64	43	24	40
2169	60	40	22	37
2187	71	31	29	47
2189	64	43	24	40
2237	50	38	27	36

TABLE 4

Mean paired affinity-values of the varieties of Silphium integrifolium *for the intravarietal comparisons*

var. *integrifolium*	var. *neglectum*	var. *deamii*
69.36	67	74.61

A one-way analysis-of-variance test was performed on the three intravarietal comparison groups. The null hypothesis was that there were no significant differences in the means of the three varieties. The mean paired affinity-values of these varieties are listed in Table 4. The F-ratio value was not significant at the 1% level of confidence; therefore there is no significant difference among the mean paired affinity-values of these varieties. These data indicate that the varieties are equally homogeneous with respect to chromatography.

TABLE 5

Mean paired affinity-values for intravarietal and intervarietal comparisons of varieties of Silphium integrifolium

var. *integ.* and var. *integ.*	var. *integ.* and var. *neg.*	var. *integ.* and var. *deamii*	var. *neg.* and var. *neg.*	var. *neg.* and var. *deamii*	var. *deamii* and var. *deamii*
69.36	74.28	70.98	67	74.43	74.61

A one-way analysis-of-variance test was performed on the intravarietal comparison groups and the corresponding intervarietal comparison groups. All of the mean paired affinity-values shown in Table 5 were compared to determine whether they were equal, i.e., whether they were equally homogeneous. The null hypothesis was that there were no significant differences in the mean paired affinity-values in these groups. The F-ratio value was not significant at the 1% level; therefore these data also indicate that the varieties are equally homogeneous with respect to chromatography.

TABLE 6

Results of Duncan's Multiple Range Test for significant differences between mean paired affinity-values of interspecific comparisons between varieties of Silphium integrifolium *(a line connects means between which there is no significant difference)*

S. integrifolium and *S. asperrimum* #1133	*S. integrifolium* and *S. speciosum* #161	*S. integrifolium* and *S. asperrimum* #1166	*S. integrifolium* and *S. speciosum* #203
60.06	42.61	38.56	26.11

A one-way analysis-of-variance test was performed by comparing *Silphium integrifolium* with the two closely related species, *S. asperrimum* and *S. speciosum.* The mean paired affinity-values were obtained by comparing each representative of *S. integrifolium* with each of the two representatives of *S. asperrimum* and *S. speciosum.* Additional representatives of *S. asperrimum* and *S. speciosum* would

TABLE 7

Characterization of spots found on chromatograms of Silphium integrifolium, S. asperrimum, *and* S. speciosum

Spot	No Reagent		NH_4OH		PMA+NH_4OH	
	Visible Light	UV Light	Visible Light	UV Light	Visible Light	UV Light
A	Green	Green	Green	Green	Green	Green
B	Brown	Blue	Brown	Blue	Brown	Blue
C	Brown	———	Yellow	———	Gray	———
D	Brown	———	Yellow	———	Gray	———
E	Brown	———	Yellow	———	Gray	———
F	Brown	———	Yellow	———	Gray	———
G	———	Bright Blue	———	Blue	———	———
H	———	Blue	———	Blue	———	———
I	———	Blue	———	Blue	———	———
J	———	Blue	———	Blue	———	Faint Pink
K	Brown	Blue	Yellow	Yellow	Gray	———
L	———	Bright Blue	———	———	———	———
M	Light Green	———	Brown-Green	———	Orange-Green	———
N	Faint Brown	———	Faint Yellow	———	Faint Gray	———
O	———	Blue	———	Blue	———	———
P	———	Faint Blue	———	Faint Blue	———	———
Q	———	Blue	———	Blue	———	———
R	———	Green	———	———	Faint Gray	———
S	———	Light Pink	———	Faint Pink	———	———
T	———	Faint Blue	———	Faint Blue	———	———
U	———	Blue	———	Blue	———	Faint Pink
V	———	Bright Blue	Light Yellow	Blue-Yellow	Gray	———
W	———	Bright Blue	———	Bright Blue	———	Light Blue
X	———	Light Green	Faint Yellow	———	Faint Gray	———
Y	———	Green	Light Yellow	———	———	———

have been used, but no others were available. The null hypothesis was that there was no significant difference in the means of these paired affinity-values. This hypothesis was rejected because the F-ratio was highly significant (1% level). Duncan's Multiple Range Test was used to determine which means were significantly different from each other. The results of this test are presented in Table 6. The mean paired affinity-values of *S. speciosum* #161, *S. integrifolium*, *S. integrifolium*, and *S. asperrimum* #1166 are not significantly different from each other, but all of the others are significantly different from each other.

RESULTS AND DISCUSSION

Morphologically *Silphium speciosum* and *S. asperrimum* are more closely related to *S. integrifolium* than are any of the other species of *Silphium*. The morphological similarity is quite obvious and has led to the mislabeling of speci-

TABLE 8

List of chromatographic spots and plants in which they were observed (see fig. 8). (Numbers along the top margin are representatives of Silphium integrifolium)

	63	147	148	148–2	158	160	218	284	2084	73	162	219	276	1104	2169	2187	2189	2237
A	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
B	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
C	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
D	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
E	+	+	+	+	+	+	+	+	+	+	+	•	+	+	+	+	+	+
F	+	•	•	+	•	•	+	•	•	•	+	•	•	•	•	•	•	•
G	+	+	•	+	+	+	+	+	+	+	+	+	+	+	+	+	+	•
H	+	+	+	•	•	+	•	+	+	•	+	•	+	+	+	•	+	+
I	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
J	+	+	+	+	+	+	+	+	•	+	+	+	+	+	+	+	+	+
K	•	•	•	•	+	+	+	+	•	•	+	+	+	+	+	+	+	•
L	+	+	+	•	•	•	+	•	•	•	•	•	•	•	+	•	+	+
M	+	•	•	•	•	+	•	•	•	•	•	•	•	•	•	•	•	•
N	•	•	•	•	•	+	•	•	•	•	•	•	•	•	•	•	•	•
O	•	•	•	•	•	+	+	+	•	•	+	+	+	+	+	+	•	•
P	•	+	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Q	•	•	•	•	•	•	•	•	•	•	•	+	•	•	•	•	•	•
R	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	+	•	•
S	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	+	•	•

TABLE 9

List of chromatographic spots and plants in which they were observed (see fig. 8). (Numbers along the top margin are representatives of Silphium asperrimum *and* S. speciosum)

	S. asperrimum		*S. speciosum*	
	1133	1166	203	161
A	+	+	+	+
B	+	+	+	+
C	+	•	•	+
D	+	•	•	•
E	+	•	•	•
F	•	+	+	+
G	+	•	•	+
H	•	+	•	•
I	+	+	+	+
J	+	+	+	+
K	+	+	•	•
L	•	•	•	•
M	•	•	•	•
N	•	•	•	•
O	•	•	•	•
P	•	•	•	•
Q	•	•	•	•
R	•	•	•	•
S	+	•	+	+
T	+	•	+	•
U	+	+	•	+
V	•	+	•	•
W	•	•	+	•
X	•	•	+	+
Y	•	•	+	•

mens in a few instances. Historically *S. speciosum* has been considered to be a *β-laeve*, and by Benke (1932) who called it *S. intergrifolium* var. *mesochorum*.

Cytological evidence reinforces the morphological evidence. All three species are in the B Group of chromosome end-arrangement. Hybrids between *Silphium integrifolium* and *S. asperrimum* and between *S. integrifolium* and *S. speciosum* exhibit normal pairing during meiosis. This pairing denotes considerable similarity in genetic material among these species.

The chromatographic data obtained indicate a degree of similarity among *silphium integrifolium*, *S. asperrimum*, and *S. speciosum*. As would be expected, these data show that the varieties of *S. integrifolium* are more similar to each other than they are to the two related species, and that *S. integrifolium* is a rather homogeneous species.

Even though the ranges of the three species overlap, and hybridization can and does occur at least occasionally, each species maintains its integrity. The isolating mechanisms which prevent widespread hybridization have not been determined. The range of *Silphium integrifolium* is more extensive than are those of *S. speciosum* and *S. asperrimum*. Putative hybrids between *S. intergrifolium* and *S. speciosum* (Mohr s.n., Hasse s.n., French s.n.) and between *S. integrifolium* and *S. asperrimum* (Morre 450488, Kellogg s.n., Eggert s.n.) have been collected. A number of specimens have been obtained in Missouri which appear to be hybrids or backcrosses involving *S. integrifolium* and *S. speciosum* (Kellogg 1300, Douglas s.n., Eggert s.n., Steyermark 1465, Sherff 726).

The intraspecific hybridization studies indicate that there is no reproductive isolation among the varieties of *Silphium integrifolium*. Numerous crosses involving all of the varieties except *S. integrifolium* var. *gattingeri*, which was not available, were made with little difficulty.

Plant #218, which was collected in Hardin County, Tennessee, is somewhat puzzling. Morphologically, it is more like *Silphium integrifolium* than any other species, but it is somewhat similar to *S. asteriscus* ssp. *latifolium*. It is interesting that plant #218 is the only representative of *S. integrifolium* which belongs to chromosome end-arrangement Group A, to which *S. asteriscus* ssp. *latifolium* also belongs. The plant was collected within the general range of *S. asteriscus* ssp. *latifolium*, which occurs primarily in the northern two-thirds of Alabama. The chromatographic profile of plant #218 does not differ significantly from that of the other representatives of *S. integrifolium*. However, no chromatographic profile of *S. asteriscus* ssp. *latifolium* is available.

The study shows that the varieties of *Silphium integrifolium* are not significantly different chromatographically. This species is uniform as indicated by chromatography.

Silphium integrifolium is apparently a relatively young species that has not yet differentiated into higher intraspecific taxa such as subspecies. Its distribution is approximately the same as that of the tall grass prairie of the United States, and one could infer that the species originated somewhere within this area.

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